

Crop science experiments designed to inform crop modeling

Peter Q. Craufurd^{a,*}, Vincent Vadez^a, S.V. Krishna Jagadish^b, P.V. Vara Prasad^c, M. Zaman-Allah^a

^a International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502324, India

^b International Rice Research Institute, Los Banos, Philippines

^c Department of Agronomy, Kansas State University, Manhattan, KS, USA

ARTICLE INFO

Article history:

Received 13 March 2011

Received in revised form 15 August 2011

Accepted 1 September 2011

Keywords:

Crop models
Crop physiology
Temperature
Carbon dioxide
Water stress
Transpiration

ABSTRACT

Crop growth simulation models are a useful tool to assess the impact of environment, crop management, genetics and breeding strategies, as well as climate change and variability on growth and yield. Any crop science experiment that measures key physiological processes, tests these productive processes, their interaction with other processes, environment, and intra- and inter-specific variation, is valuable to inform and refine crop simulation models. This paper focuses on crop science experiments in three key areas—crop development, seed or fruit-set at high temperature, and water use—illustrating some of the experiments used to understand key processes and, equally importantly, quantify these processes for crop models in a robust and repeatable manner. One particularly useful experimental method for determining stages of development responsive to photoperiod and temperature (the main drivers of ontogenic development), and sensitive to abiotic stresses such as temperature extremes and water deficit, is transfer experiments between different environments or treatments. Once sensitive stages are defined, then responses and genotypic differences can be accurately quantified. Understanding and modeling transpiration, and particularly genotypic differences in processes affecting transpiration is also key process for crop modeling. Experiments to determine genotypic differences in soil water availability thresholds that control when transpiration is reduced, relations between transpiration and vapor pressure deficit (VPD), and patterns of soil water uptake are also described along with new insights from this work. One of the biggest constraints to improving models with crop science experiments—and exploiting advances in genomics—is the limited capacity to phenotype traits and physiological mechanisms. Most crop science experiments have quantified responses in only a limited number of genotypes and the diversity of genotypic responses is not well represented. Today there is an increased demand for good quality phenotyping which can serve both genomics and modeling, and there is an urgent need to re-invest in crop physiology for high quality phenotyping.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Crop models (e.g. DSSAT, Jones et al., 2003; APSIM, Keating et al., 2003; Oryza, Matthews et al., 1995; GLAM, Challinor et al., 2004; INFOCROP, Agrawal et al., 2006), mainly mechanistic or process-based (as opposed to statistical or empirical) have frequently been used to analyze and assess the value of physiological traits (Sinclair et al., 2005, 2010), to understand genotype \times environment \times management ($G \times E \times M$) interactions (Messina et al., 2009), and more recently to examine impacts of climate change on yield (Nelson et al., 2010). Indeed, the need to accurately model effects of climate change on crop yields has stimulated renewed interest in crop modeling, more especially understanding, quantifying and modeling genetic variation in key

traits or processes across scales. For example, many climate change impact studies have suggested that temperature will be a major constraint (Lobell and Field, 2007), stimulating greater interest in understanding and quantifying responses to extreme temperatures (Jagadish et al., 2007, 2008, 2010). Furthermore, the quantum leap in our technical ability to identify QTLs or genes has also led to more interest in modeling gene \times trait \times phenotype interactions (Cooper et al., 2005), though this is very much limited by our capacity to understand and phenotype key processes. Likewise, the capacity of models to simulate 'management', especially management practices associated with soil nutrients and to some extent rainwater harvesting and conservation practices, is very limited.

Crop models are generally designed around four key components: plant development, carbon capture, water capture and nitrogen and phosphorus capture. Plant development or phenology determines the timing and duration of key developmental events, notably flowering (anthesis), and as such provides the framework within which processes of carbon, water and nutrient capture and

* Corresponding author. Tel.: +91 40 3071 3691; fax: +1 91 40 3071 3074.
E-mail address: p.craufurd@cgiar.org (P.Q. Craufurd).

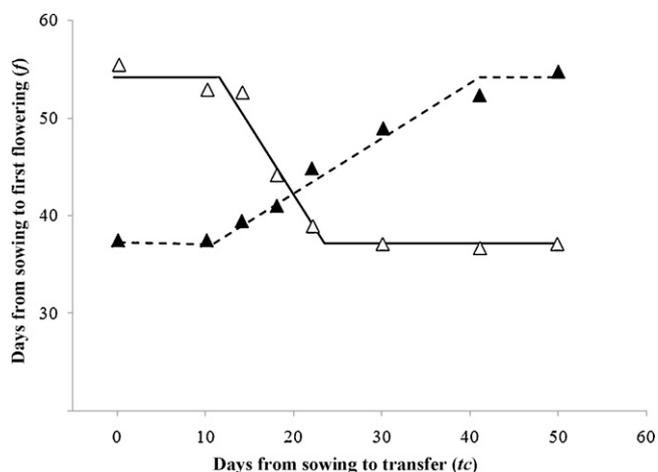


Fig. 1. Reciprocal transfer experiment to determine duration of temperature and photoperiod-sensitive phases in soybean cv Biloxi was transferred from long to short (\blacktriangle) and short to long (\triangle) days.

Redrawn from Collinson et al. (1993).

use occur. Matching crop development to the available soil moisture supply, as well as avoiding other environmental constraints such as cool or hot temperatures (Flower, 1996), is a key determinant of adaptation today and will continue to be important in future climates. Indeed, a number of climate impact modeling studies have shown that the impact of climate change, positive or negative, is strongly related to whether crop duration is shortened or lengthened (Challinor and Wheeler, 2008a; Tao and Zhang, 2010).

Essentially, all plant processes that interact and take part in plant productive processes can be modeled and therefore, any crop science experiment that tests these productive processes, their interaction with other processes, their interaction with the environment, their intra- and inter-specific variation, is potentially useful to refine crop simulation models (Sinclair and Seligman, 2000). This paper focuses on a three key areas—crop development, seed or fruit-set at high temperature, and water use—illustrating some of the key concepts that drive research in these areas, and the types of crop science experiments used to understand key processes and, equally importantly, quantify these processes for crop models in a robust and repeatable manner. Examples of the uses of these types of information in crop models are also given where available.

2. Crop development

Phenology is a key trait for modeling as it determines the framework or timing of developmental events (emergence, floral initiation, flowering or anthesis, and physiological maturity) contributing to biomass accumulation and partitioning in any given environment. Most crop models (e.g. DSSAT, APSIM, INFOCROP) parameterize phenology by defining stages of development linked to the key developmental stages outlined above (i.e. vegetative, juvenile or basic vegetative phase; inductive or photoperiod-sensitive phase; post-inductive and/or seed-filling phase) sensitive to temperature (T) and/or photoperiod (P) (Table 1). The vegetative and post-inductive phases are basically determined by temperature through the number of leaves to be expanded and hence have similar thermal sums or accumulated cd. The photoperiod-sensitive phase is also a constant thermal sum when P is less than a critical value (≤ 11.5 h in the case of rice, a short-day species), but when P is greater than a critical value the duration of this phase is greatly lengthened, more so at warmer than cooler temperatures, or even

lengthened indefinitely for strongly P sensitive germplasm (Folliard et al., 2004).

2.1. Using field experiments to parameterize models

Phenology parameterization is generally determined experimentally by using multiple sowing dates and modeling using least squares or maximum likelihood routines to optimize the best-fit parameters within predetermined ranges (Dingkuhn, 1995; Carberry et al., 2001). The advantage of this field-based approach (though it can be done in pots) is that large numbers of genotypes can be grown (Dingkuhn, 1995; Dingkuhn and Asch, 1999) and other parameters observed for model calibration or validation. The disadvantage is that models are optimizing several parameters at once (i.e. response to temperature and photoperiod, vegetative phase duration) plus there is some correlation between T and P (and possibly other weather parameters such as relative humidity [RH]/vapor pressure deficit [VPD]), and T and P effects cannot easily be examined independently of each other. The latter effect assumes much greater importance when genotypes are to be simulated outside their natural range of P and T, especially at higher temperatures or in non-inductive photoperiods (i.e. long days for short-day plants (Clerget et al., 2004; Carberry et al., 2001)).

2.2. Controlled environment experiments to determine phase durations

The alternate approach is to use controlled environments, where T and P can be controlled independently of each other. Phase durations are typically determined using reciprocal transfer experiments (Ellis et al., 1992) wherein plants are transferred at regular intervals between long and short photoperiods, ideally at two temperatures in the sub-optimal range (Fig. 1). Such experiments determine precisely the duration of temperature and photoperiod-sensitive phases (Collinson et al., 1992, 1993; Alagarwamy et al., 1998). To date genetic variation in these phases has been determined in relatively few crop species, the best known example being rice where the vegetative phase can vary from 10 to 80 d (Vergara and Chang, 1976; Dingkuhn, 1995). In sorghum and soybean durations range from 4 to 18 d and 11 to 35 d, respectively (Alagarwamy et al., 1998; Ellis et al., 1992; Collinson et al., 1992, 1993; Sinclair and Hinson, 1992). Given that several recent impact studies have suggested that a key strategy to counter warmer temperatures shortening crop duration—and hence lowering yields—is a longer vegetative phase (Challinor and Wheeler, 2008a; Tao and Zhang, 2010), determining the full range of genetic variation in this trait is important.

2.3. Controlled environment experiments to quantify responses to temperature and photoperiod

The effects of T and P on rates of development are typically quantified by growing plants in factorial combinations of T and P. A key advantage of a factorial design is that it allows, on the one hand, for the response to temperature to be quantified under inductive conditions (i.e. where photoperiod does not affect or confound the rate of development) and, on the other hand, the affect of photoperiod to be quantified at near optimal temperature conditions (where temperature does not confound the photoperiod response). A simple three or four temperature by two photoperiod factorial will be sufficient to parameterize genotypes at sub-optimal temperatures (Erskine et al., 1990). It is worth noting here that most crop models are parameterized for photoperiod-insensitive or relatively photoperiod-insensitive genotypes (which predominate in high input agriculture) rather than for landraces or traditional farmer's cultivars which are often acutely sensitive

Table 1
Durations of the pre-inductive or vegetative (VEG), inductive or photoperiod-sensitive (PSP) and post-inductive (PIP) phases in rice cultivar Peta at two temperatures and photoperiods. VEG and PIP not determined at 11.5 h.

Mean temperature (°C)	Photoperiod	Duration in days (cd [Tb = 10 °C] in parenthesis)			
		VEG	PSP	PIP	Total
23.8	13.5	39 (533)	83 (1145)	22.8 (315)	144 (1984)
	11.5	–	19 (264)	–	81 (1102)
28.7	13.5	30 (540)	113 (2143)	20.7 (387)	163 (3047)
	11.5	–	14 (252)	–	63 (1179)

Modified from Collinson et al. (1992).

to photoperiod. For example, values up to 2100 cd h⁻¹ for cultivars from Mali (Vaksmann et al., 1998; Folliard et al., 2004) or Nigeria (Craufurd and Qi, 2001) have been recorded. In sorghum for example, until recently photoperiod-sensitivity coefficients in DSSAT spanned an equivalent thermal accumulation range of between 12 and 400 cd h⁻¹ when P is greater than the critical value (Alagarswamy and Ritchie, 1991) with a maximum value of 999 cd h⁻¹; however, a recent release now allows for much higher values for photoperiod sensitivity. As impact models become more regional in focus, and focus more on adaptation and breeding strategies, then representing 'local' cultivars in models will become more important.

Another significant difficulty comes in modeling crop development at supra-optimal temperatures ($T > T_0$, where T_0 is the optimal temperature), which as mentioned earlier is critical for climate change impact studies (Challinor and Wheeler, 2008a,b; Tao and Zhang, 2010). Optimum temperatures in maize for example vary between ecotypes from 17 to 20 °C in highland tropical types to 30 to 34 °C in lowland tropical types, with temperate types in between (Jiang et al., 1999). Ecotypes of rice, indicas and japonicas, also have warmer and cooler optimum temperatures, respectively. Among cultivars within species there may also be variation in the optimum temperature, and even a small difference (28.7 cf 30.2 °C) can make a significant difference to the impact (Tao and Zhang, 2010). The optimum temperature response will be a major determinant of whether a genotype develops faster as temperatures warm or whether development slows, with significant consequences for yield (Challinor and Wheeler, 2008a; Tao and Zhang, 2010). Existing crop models such as GLAM, DSSAT and QNUT differ in their parameterization and response to supra-optimal temperatures and hence potential impacts on yields (Challinor et al., 2007; Challinor and Wheeler, 2008b). Furthermore, there is uncertainty over whether P and T interact at supra-optimal temperatures (Craufurd and Wheeler, 2009), though this may only be important in highly photoperiod-sensitive genotypes. It should be noted here that the effect of high temperature on fruit-set in cowpea (Craufurd et al., 1998) is affected by photoperiod also (Ahmed et al., 1993).

2.4. Modeling 'alleles' and flowering pathway genes

In relation to modeling such an important trait as the timing of flowering, it is worth mentioning that there has been progress in modeling flowering time genes rather than observable and essentially whole plant morphological stages. Unsurprisingly, as flowering time is such a key and easily observable trait, there has been considerable progress in identifying flowering pathway genes (Jung and Muller, 2009) and in describing and modeling some of the networks that define these responses in Arabidopsis (Welch et al., 2004). Some existing crop models also incorporate effects of flowering time alleles within existing whole crop model frameworks (White and Hoogenboom, 2003).

2.5. Genetic variation in phase durations and responses to temperature and photoperiod

There is considerable genetic variation in photoperiod-sensitivity in most species (maize: Bonhomme et al., 1994; sorghum, Craufurd et al., 1999; soybean, Roberts et al., 1996; rice, Dingkuhn, 1995), and genetic variation for temperature responses and the length of the vegetative phase associated with ecotypes in some species (rice, Vergara and Chang, 1976; Dingkuhn, 1995; sorghum, Craufurd et al., 1999; soybean, Sinclair and Hinson, 1992). As mentioned previously, the full range of variation available in these key parameters is rarely used in crop models to explore potential adaptation to future climates, though Challinor et al. (2009) provide an exemplar on how to do this.

3. Effect of temperature on seed-set/fruit

Impacts of water stress (drought) or high or low temperature stress on crop growth and yield depend on the severity of stress, duration of stress and the plant developmental stage at which stress occurs. For crop models to predict the impacts of abiotic stresses, both water and temperature stress, it is important to determine the most sensitive stages of crop development to stress. In general for both water and temperature stress the most sensitive stages of development occur between floral or panicle development and the end of flowering (i.e. including fertilization) in both cereals and legumes (O'Toole, 1982; Claassen and Shaw, 1970). The stages of development most sensitive to high (and low) temperature are associated with the processes of microsporogenesis, anther dehiscence and fertilization in legumes (peanut, Fig. 2a, Prasad et al., 2001, 1999) and cereals (sorghum, Fig. 2b; Prasad et al., 2008a; rice, Fig. 2c; Yoshida et al., 1981).

3.1. Determining the stages of development sensitive to high temperature

The approach used in determination of sensitive stages to heat stress (Prasad et al., 1999, 2008a) is transfer experiments. In this approach plants are grown under controlled conditions in optimum and high temperature conditions until target stages of crop development are reached (e.g. 15 d before flowering in rice). Thereafter, at periodic intervals plants grown in optimum conditions are exposed to stressed environments for specified duration, before being returned to optimum conditions (and vice-a-versa).

For example, using this approach it was identified that in peanut fruit-set was most sensitive to high temperature stress during the day at 4d prior to anthesis and on the day of anthesis (Fig. 2a: Prasad et al., 2001). Similarly, in rice (Fig. 2c: Yoshida et al., 1981), and sorghum (Prasad et al., 2008a) plants are sensitive to high temperature about 9 days before anthesis and at anthesis (Fig. 2), with the latter stage, as in peanut, being more sensitive to high day temperature. These two stages in both peanut and the cereals coincide with microsporogenesis and anther dehiscence/fertilization,

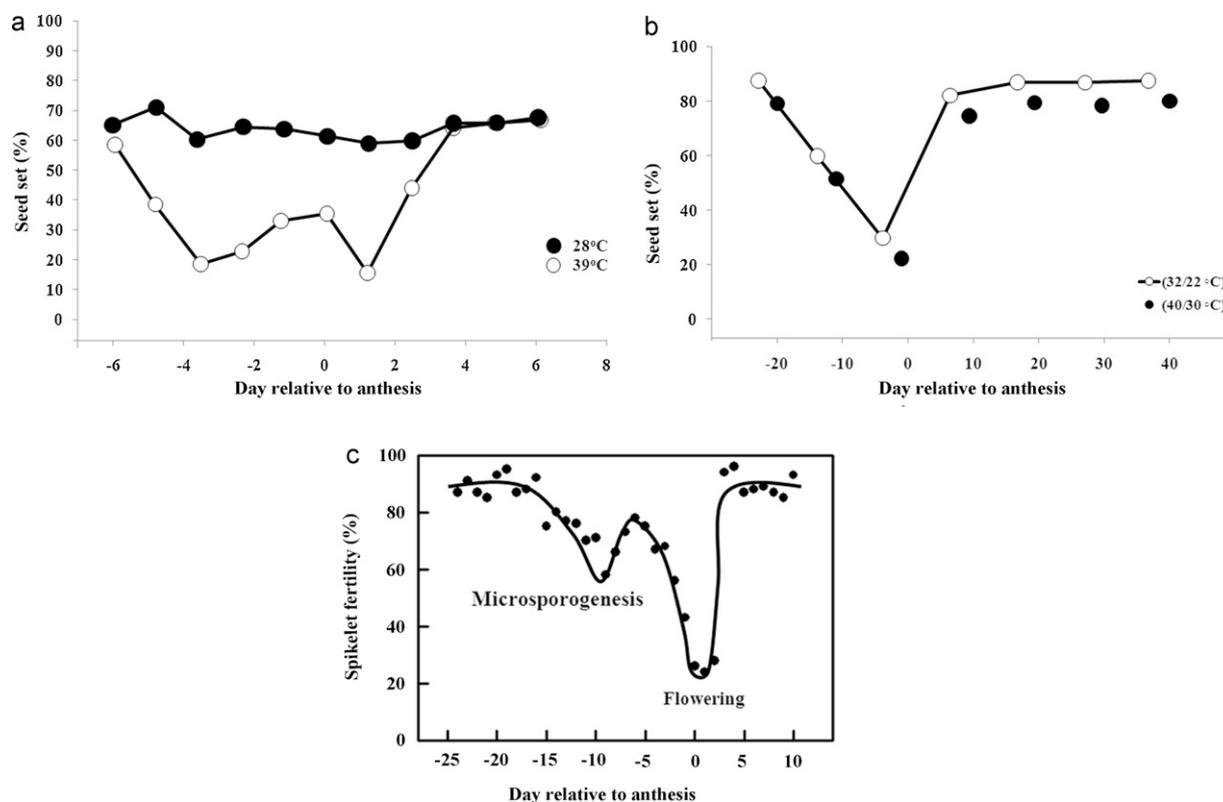


Fig. 2. Sensitivity to high temperature at flowering in (a) peanut (b) sorghum and (c) rice.

Redrawn from Prasad et al. (2000, 2008a), and Yoshida et al. (1981).

respectively. In contrast, high night temperatures seem to affect microsporogenesis more than anthesis (Ogunlela and Eastin, 1984; Mohammed and Tarpley, 2009). Sensitivity to high temperature in terms of seed or fruit-set does not extend much beyond fertilization; indeed rice spikelets are not affected by high temperature about 1 h after anthesis (Jagadish et al., 2007). These types of experiments can also be carried out in the field by covering with suitable materials to cool or warm plots/plants (Nielsen and Hall, 1985), or even by multiple sowing dates accompanied by careful recording of flowering dates and environmental conditions at flowering (Dingkuhn, 1995; Nagarajan et al., 2010).

Transfer experiments in controlled environments can be further refined to study the timing of high temperature during the diurnal cycle where it is suspected that key events such as fertilization occur during the early morning or even in the night prior to dawn (Mutters and Hall, 1992). In peanut, for example, it is the temperature during the first 6 h of the day that determines fruit-set (Prasad et al., 2000).

3.2. Quantifying responses of seed-set to high temperature

Once the stages most sensitive to temperature are identified, it is important to know how fruit or seed-set responds to the intensity and duration of stress when applied at these stages of development. Again, controlled environments (Prasad et al., 2000, 2008a,b; Wheeler et al., 1996; Yoshida et al., 1981) or field experiments with multiple sowings and careful analysis (Dingkuhn, 1995) can be used to quantify responses to temperature. The example of peanut (Fig. 3a, Prasad et al., 2000) is a very typical response of seed or fruit-set to temperature, exhibiting a critical threshold (typically about 33–35 °C) in many tropical crops such as sorghum, rice and 24–27 °C in temperate crops such as wheat (Wheeler et al., 1996) and a negative linear response to increasing temperature above

this to a maximum value. Other traits such as pollen number, pollen germination and pollen tube growth can be modeled the same way. Several crop models incorporate these responses (Oryza, Matthews et al., 1995; AQUACROP, Steduto et al., 2009; GLAM; Challinor et al., 2005).

Transfer experiments can also be used to determine the duration and intensity of stress by exposing transferred plants to varying durations and intensities (Prasad et al., 1999; Jagadish et al., 2007). These experiments have generally suggested that for fruit or seed-set there is no interaction between duration and intensity of temperature and hence the combined response can be modeled by a cumulative temperature function (Fig. 3b). Thus in rice the greater the exposure to temperatures >33 °C during flowering, the lower the seed-set.

3.3. The importance of timing

Another important factor alluded to above determining the appropriate temperature to use for modeling high temperature events is the timing of anthesis and fertilization. From transfer experiments in peanut it was determined that it was temperature in the first 6 h of daylight (in a 12 h photoperiod) rather than the average day temperature or temperature during the second 6 h that determined fruit-set (Prasad et al., 1999). This is associated with the timing of fertilization, which probably occurs early in the morning in peanut. Challinor et al. (2005) used the temperature during the first 6 h of the day in their evaluation of tolerance to high temperature in peanut in India under climate change scenarios. Similarly, in rice there is variation in the timing of peak flowering among genotypes, which maybe from early morning through till midday (Fig. 4; Jagadish et al., 2008; Prasad et al., 2006a,b). So while maximum temperature maybe the appropriate 'signal' temperature to use for some cultivars or species, in others early or mid-morning

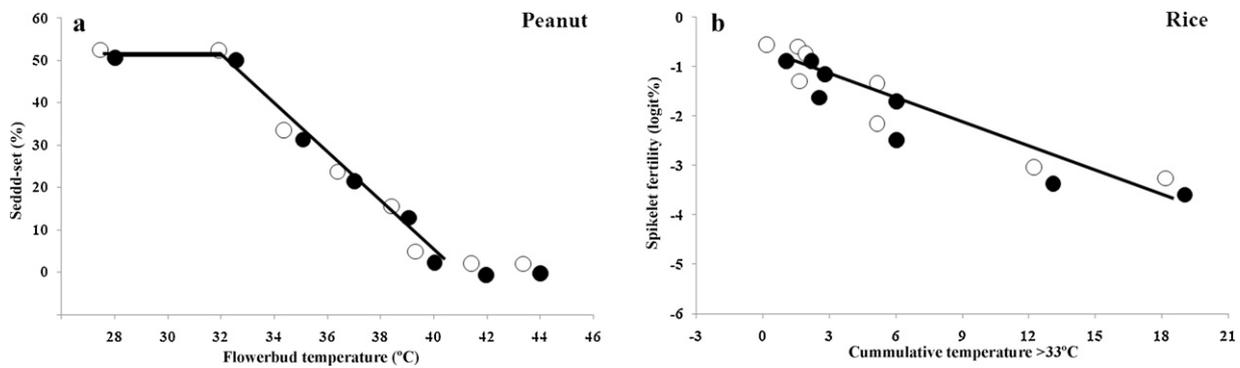


Fig. 3. Effect of temperature on seed (fruit)-set in peanut (a) and relation between spikelet fertility (seed-set) and cumulative temperature >33°C over 5 d flowering period in rice (b).

Redrawn from Prasad et al. (2000) and Jagadish et al. (2007).

Table 2

Genetic variation in spikelet fertility (seed-set) of rice exposed to either 2 or 6 h of high temperature at anthesis.

Genotype	Tissue temperature (°C)			
	29.6		36.2	
	2 h	6 h	2 h	6 h
N22	94.7	95.6	85.7	63.7
Bala	87.5	89.8	65.1	40.6
Co 39	89.5	86.1	64.5	40.5
Azucena	62.5	66.1	7.9	2.9
CG14	86.1	89.6	43.7	19.1
IR64	87.7	93.2	67.1	18.7
Moroberekan	81.7	83.3	4.0	6.4
WAB 56-104	65.8	94.6	31.9	19.2

Modified from Jagadish et al. (2008).

temperature maybe more appropriate. A number of models use algorithms that calculate 3 hourly mean temperature from daily maximum and minimum temperature and so it would not be too difficult to use an appropriate morning or early morning temperature at anthesis.

3.4. Genetic variation in seed-set at high temperature

From the studies cited above genetic variation in seed or fruit-set has been determined in a number of crop species, including rice (Table 2; Yoshida et al., 1981; Prasad et al., 2006a,b; Jagadish et al., 2008), cowpea (Hall, 1993), peanut (Craufurd et al., 2003).

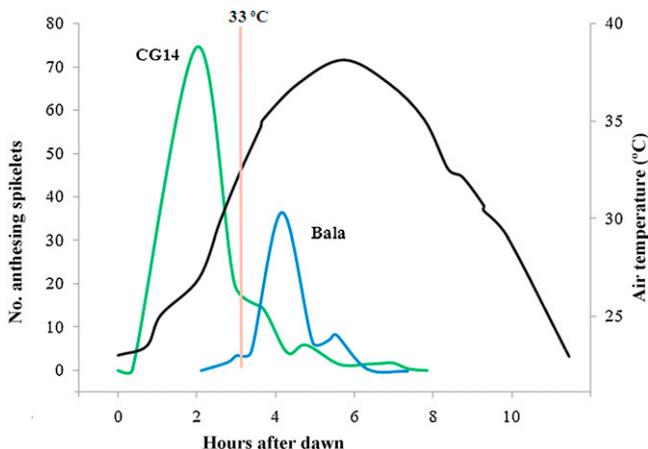


Fig. 4. Flowering time and air temperature relative to dawn in African rice (CG14) and Asian rice (Bala). Authors unpublished data.

The genetic variation in peanut and rice has been used in modeling studies (Matthews et al., 1995; Challinor et al., 2005). Genetic variation in the response to temperature of traits contributing to seed or fruit-set, namely pollen germination and pollen tube-growth, has also been documented in several species (see Salem et al., 2007 for soybean and refs therein).

4. Effects of diurnal temperature

Understanding impacts of climate change and climate variability needs improved understanding of impacts of increased mean temperatures, especially minimum or night temperature (Peng et al., 2004; Nagarajan et al., 2010; Welch et al., 2010) as well as impacts of short term extreme temperatures (Wheeler et al., 2000). Crop science experiments are also critical to determine the optimum and ceiling temperatures for yield formation and response between optimum and ceiling temperatures. Such information serves as critical input to crop models. Season long temperature responses of yield formation in various crop species under ambient and above ambient CO₂ were identified for important cereals (rice, Baker et al., 1996, wheat, Wheeler et al., 1996; and sorghum, Prasad et al., 2006a,b) and legumes (dry bean, Prasad et al., 2002; groundnut, Prasad et al., 2003; soybean, Baker et al., 1989) using controlled experiments.

Critical temperatures for vegetative and reproductive yield formation for a few important crops are given in Table 3. These data indicate: significant variation in optimum temperatures for development and yield (or growth), and between vegetative and reproductive yield; and (ii) large differences between crop species, most especially between temperate and tropical species.

5. Effects of temperature and CO₂ on seed-set—the importance of tissue temperature

In future climates temperature changes will be accompanied by elevated CO₂. Thus, it is important to understand the interaction effects of temperature and CO₂, especially as most impact studies suggest higher temperatures will offset any CO₂ fertilization gains in C₃ crops (e.g. Long and Ort, 2010; Lobell and Field, 2007; Nelson et al., 2010). Some reports in the literature suggest that elevated CO₂ causes greater sensitivity of spikelet fertility to heat stress, and temperature-induced decreases in pollination, seed set, pod yield, seed yield, and seed HI were the same or even greater at elevated than at ambient CO₂ levels in kidney bean and sorghum (Prasad et al., 2002, 2006a,b) and in rice (Nakagawa et al., 2003). The ceiling temperatures for fruit-set were about 2°C lower in rice, bean and sorghum (Prasad et al., 2002, 2006a,b; Matsui et al., 1997).

Table 3

Optimum temperature for reproductive development, optimum temperature range for vegetative and reproductive yield, and the ceiling temperature (all in °C) at which seed or fruit yield falls to zero in a range of crop species.

Crop	Optimum temperature for reproductive development	Optimum temperature range for vegetative yield	Optimum temperature range for fruit or seed yield	Ceiling temperature for yield
Wheat	26	20–30	15	34
Soybean	26	25–37	22–24	39
Cotton	28–30	34	25–26	35
Temperate sorghum hybrid	31	26–34	25	35
Groundnut	29–33	31–35	20–26	39
Rice	33	33	23–26	35–36

Modified from Hatfield et al. (2008).

However, the impact of high temperature on seed or fruit-set is better related to tissue temperature than ambient air temperature. Several field studies have shown a good relationship between canopy temperature and sterility (Cohen et al., 2005; O'Toole, 1982). Under ambient CO₂ conditions, tissue temperature can be up to 4 °C lower than air temperature (Prasad et al., 1999; Jagadish et al., 2007) and this is why some studies quantify seed set against tissue temperature. At higher CO₂, stomatal conductance is decreased leading to lower transpirational cooling and increased canopy temperature (Matsui et al., 1997, 2001). Thus in studies of high temperature by CO₂ effects on seed-set, the commonly observed interaction or greater reduction in seed-set at high CO₂, may in fact be associated with higher tissue temperature at high CO₂ (Fig. 5). Therefore what matters for modeling is to accurately calculate tissue or canopy temperature.

6. Transpiration

Plant growth depends on the availability of water in the soil profile and transpiration or plant water use is a key parameter in all crop models. Most models simulate the extraction of available water (generally defined as water between the upper and lower drained limits) via a demand function and partitioning between transpiration and soil evaporation. Many models also use the concept of Fraction of Transpirable Soil Water (FTSW) as a modifier of other key processes such as leaf expansion or radiation use efficiency. The FTSW threshold for decline in transpiration is determined by exposing plants to controlled and progressive soil water depletion under conditions of no/minor evaporation from soil surface (Fig. 6). The daily transpiration of these plants is normalized by dividing each individual transpiration value by the mean of the transpiration of the well watered control. Then the FTSW values

representing the portion of remaining volumetric soil water available for transpiration on each day of the experiment are plotted against the normalized daily transpiration rate (NTR) values of the water stressed plants. A plateau regression procedure on the NTR response curve as a function of FTSW provides estimate of FTSW thresholds (where NTR starts declining) for each given genotype (Ray and Sinclair, 1998).

In a situation where water is limited, for example by stopping irrigation, it is well established that plant response to the imposition of a water stress will go through three different stages (Sinclair and Ludlow, 1986; Fig. 6): Stage I where there is sufficient moisture in the soil profile to sustain transpiration-demand by the leaves and therefore during that stage, the transpiration of plants exposed to water deficit is equivalent to the transpiration of plants maintained under fully irrigated conditions; (ii) Stage II, where the roots can no longer supply all transpiration demand by the leaves; under such conditions, to avoid loss of turgidity and/or cavitation in the xylem vessels, the stomata partially close to match transpiration with water supply; (iii) Stage III where the plants have extracted all water available in the soil profile and where, as a consequence, stomata are fully closed; that stage corresponds to the beginning of a survival stage, since there is no longer any photosynthetic activity, and it is estimated that this stage is reached when the transpiration of water deficit plants falls below 10% of those maintained under fully irrigated conditions.

Using this framework, it is particularly critical to understand when plants shift from Stage I to Stage II. Indeed, for a productivity point of view, Stage II marks the beginning of a reduced production of biomass compared to a fully irrigated plant. Conversely, from a water saving point of view, the beginning of Stage II would also mean the beginning of water-saving measures by plants. So, depending on the drought scenario or pattern, a knowledge of this threshold is important; under a long drought spell an early passage into Stage II might help; in contrast, under short, intermittent drought spells remaining in Stage I would maximize production.

There exists genotypic variation in the level or soil moisture threshold where the transpiration of plant starts declining (when plant go from Stage I to Stage II; see Fig. 6) in soybean (Vadez and Sinclair, 2001); pearl millet (Kholova et al., 2010a), peanut (Bhatnagar-Mathur et al., 2007; Devi et al., 2009), and chickpea (Zaman-Allah et al., 2011a). The range of these thresholds varies among species and the developmental stage at which the assessment is done. For example in chickpea and pearl millet the FTSW threshold at full vegetative stage varies from 0.56 to 0.25 and from 0.50 to 0.30, respectively (Zaman-Allah et al., 2011a; Kholova et al., 2010a). Differences in TE might also be closely related to how plants respond to soil drying. High TE genotypes are likely to maintain gas exchange until the soil is dryer (low FTSW threshold) than low TE genotypes (Devi et al., 2010). However, under conditions of terminal stress, the high TE genotypes may suffer from rapid soil moisture depletion with a subsequent negative impact on yield.

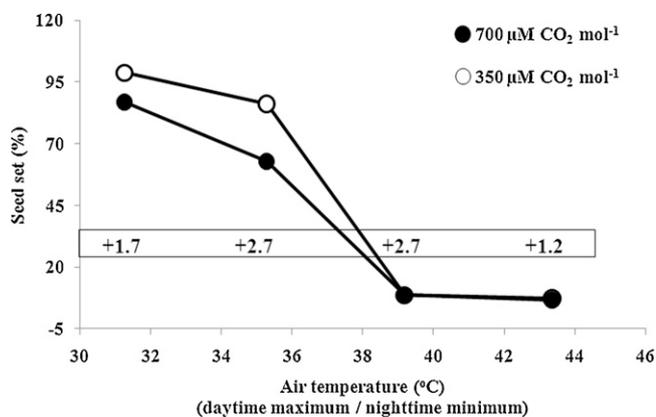


Fig. 5. Effect of temperature on seed-set in sorghum at two levels of [CO₂]. The difference in tissue temperature between ambient and high [CO₂] is also shown. Redrawn from Prasad et al. (2006a).

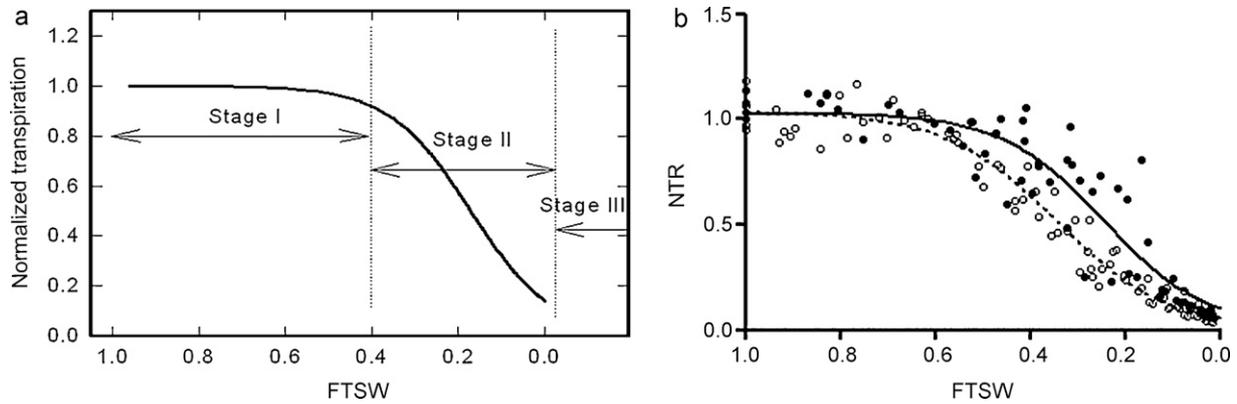


Fig. 6. (a) Basic response of plant exposed to water deficit and (b) relationship between the normalized transpiration ratio (NTR) and the fraction of transpirable soil water (FTSW) of in two chickpea genotypes contrasting for terminal drought tolerance (sensitive line, black symbols and solid lines; tolerant line, open symbols and dashed lines) grown under outdoors conditions.

For example, it was recently found that the transpiration of several independently determined terminal drought tolerant lines of chickpea exposed to water deficit declined at higher level of soil moisture than the transpiration of terminal drought sensitive lines (Zaman-Allah et al., 2011a).

The importance of these results lays in the fact that tolerant lines have early signals of a forthcoming stress. An earlier decline in transpiration then contributes to water saving, which may be available for the grain filling period, and this is relevant in a terminal water stress situation (an unrelieved water stress that takes place from approximately flowering onwards). This type of information has been used in crop simulation modeling to predict the effect on yield across several locations where chickpea is grown (Soltani et al., 2000), and has shown a benefit to yield in maize and sorghum (Sinclair and Muchow, 2001).

6.1. Response of plant transpiration to environmental conditions

Besides radiation, an important driver of plant transpiration is the evaporative demand of the atmosphere. It is particularly important in a context of plants exposed to water deficits. The evaporative demand, which is proxied by the vapor pressure deficit (VPD), depends in part on the air temperature and relative humidity (RH). When the VPD is high, i.e. if RH is low and/or the air temperature is high, the transpiration is driven up. Crop simulation models in their calculation of transpiration usually consider transpiration to be a linear response to VPD. However, recent experimental work shows that the response of different crops and genotypes vary (Fig. 7). For instance, it was shown recently that the slope of

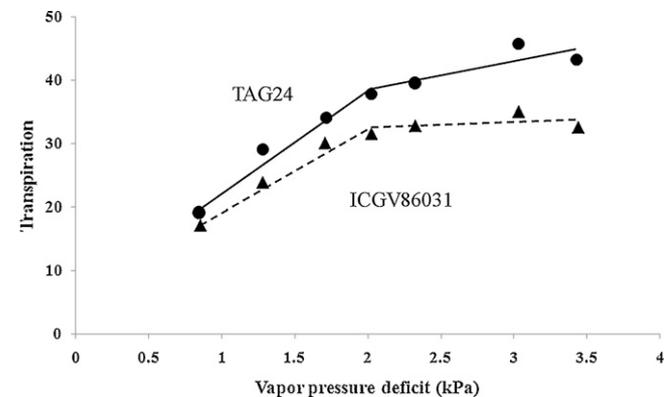


Fig. 7. Transpiration response to a gradual increase in the vapor pressure deficit in two groundnut genotypes. Authors unpublished data.

the transpiration response to VPD varies in chickpea (Zaman-Allah et al., 2011a). Also there is now accumulating evidence that the pattern by which transpiration increases at high VPD (beyond 2 kPa) differs between genotypes, e.g. in soybean (Sinclair et al., 2008), sorghum (Gholipour et al., 2010), peanut (Devi et al., 2010), pearl millet (Kholova et al., 2010b). In these crops, certain genotypes do not follow a linear increase in transpiration in response to the VPD. Indeed, above a genotype-specific VPD threshold or transpiration breakpoint (VPD value where the slope of transpiration response to VPD changes), there is a reduction in the rate of transpiration due to partial stomata closure. As a consequence, carbon fixation also declines in genotypes having a transpiration breakpoint. However, these genotypes save water for later. In contrast, genotypes that do not show any break point maintain carbon fixation, albeit at a high water cost as water use efficiency is inversely related to the VPD (Bierhuisen and Slatyer, 1965).

The transpiration response to VPD is therefore an important trait since it represents a potential water saving mechanism. This trait has been used in crop simulation modeling and these simulations suggest that limiting transpiration to 4mm d^{-1} would increase yield under water limited conditions in sorghum in Australia (Sinclair et al., 2005). Similarly, the VPD response trait outlined above was simulated in soybean and showed significant yield advantage across most of the US soybean growing areas (Sinclair et al., 2010).

7. Pattern of water extraction

Another critical component of crop simulation modeling, especially in the context of water limitation, is the rate of root growth. While there is a lot of knowledge and refinement on the mechanics of plant productive processes related to the aboveground part, there is relatively little work on the use of modeling for the belowground part. There has been some work to assess the water extraction parameters in relation to quantity and density of roots in different crops (Dardanelli et al., 1997, 2004). However, there is still a lot of discrepancy in the relationship between root growth characteristics and the capacity of plants to extract water. Some reports have shown that root length density and water uptake are related (Passioura, 1983; Monteith, 1986; Lafolie et al., 1991). In contrast, other studies report poor relations between water uptake and root length density across cereals and legumes (Hamblin and Tennant, 1987; Dardanelli et al., 1997; Katayama et al., 2000; Amato and Ritchie, 2002). In consequence, one current limitation of crop simulation modeling is their dependence on a root growth parameter to determine the amount of available soil water.

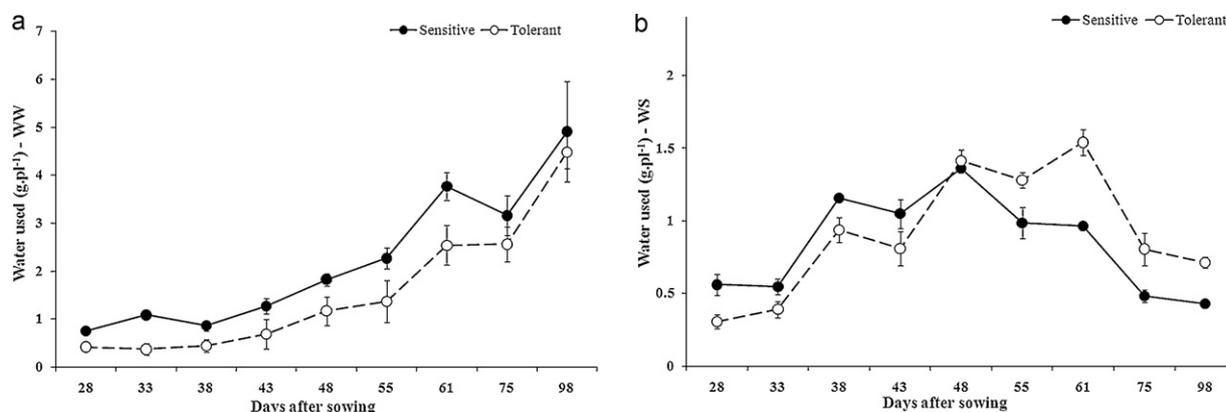


Fig. 8. Variation of water uptake profile in two chickpea genotypes contrasting for the drought stress index (DTI) under terminal drought stress (sensitive line, closed symbols and solid lines; tolerant line, open symbols and dashed lines) and grown under (a) well watered and (b) water stress conditions. Water stress imposition was initiated by giving a last irrigation at 23 DAS. The water extraction values are those for the period finishing at the date when data are plotted. For instance, water extracted at 28 DAS corresponds to that in the period between 23 and 28 DAS.

Redrawn from Zaman-Allah et al. (2011b).

On-going work at ICRISAT is acquiring better knowledge on the role of roots in the context of a water limitation, where the focus is not on acquiring knowledge on the root morphology but on obtaining data on the pattern of water use from a soil profile in plants that are grown in a field-like situation (Fig. 8). For this, a lysimetric system is used (Vadez et al., 2008; Ratnakumar et al., 2009) with plants growing in long and large PVC tubes (1.2 or 2.0 m depending on crops), which provide each plant with a soil profile equivalent to the one available in a real field situation. This system has been used to assess the relation between rooting density and water extraction in groundnut and has shown both a lack of relationship, or a highly significant relationship (Vadez et al., 2007). It has been shown also that in chickpea exposed to terminal stress, differences in rooting do not lead to differences in seed yield. Rather, the pattern of water use from the soil profile explained the differences in seed yield, with sensitive entries during the vegetative stage, and extracting more water than the sensitive entries during the pod filling stage. Similar results, i.e. the importance of water extraction at critical stages of crop development, have been found in groundnut (Ratnakumar et al., 2009) and in pearl millet.

Experiments using this system could be very useful to improve crop simulation models with regard to their water relation feedback loops. For instance, the knowledge of the moisture threshold where transpiration declines (seen above) and of the pattern of water use from lysimetric profile would allow one to rigorously measure the real rate of growth of the root water extraction front, which could then be fed to tune the water extraction loop in crop simulation models. In addition, equipping the lysimeters with time-domain reflectometry access tubes would also allow to compare a pattern of water extraction with a profile of water extraction and would then allow to refine crop models with regards to the soil extraction depth.

8. Discussion

One of the major, if not the major, constraint to improving models with crop science experiments is the limited capacity to phenotype traits and mechanisms. Most crop science experiments have quantified responses in only a limited number of genotypes, and in many cases these genotypes are 'standard' improved cultivars chosen for their popularity rather than a diversity of traits. As we have suggested in this article, for many important traits the extent of genetic variation has either not been adequately described

and/or not been incorporated into models. The limitation in phenotyping is perhaps best seen in the light of advances in molecular genetics, which has hugely increased our ability to identify genes (see for example the large scale high throughput phenomics facility in Adelaide <http://www.plantaccelerator.org.au>) and ultimately the mechanisms responsible. One area where genomics (and other 'omics') have greatly increased our understanding of gene networks controlling an important trait is for flowering time, particularly the photoperiod and vernalisation pathways, though less progress has been made on temperature pathways controlling flowering. Although there has been progress in modeling flowering-time gene networks in *Arabidopsis* (Welch et al., 2004), ironically flowering-time or phenology has been one trait that farmers and plant breeders have been able to successfully manipulate over millennia, though fine-tuning this trait for specific environments may well be useful. Nonetheless, the exponential increase in genomic platforms, along with the demand for climate change impact models, has highlighted the need to re-invest in crop physiology and phenotyping.

There is evidence that responses of plants to environmental change under controlled conditions often differ from those found under natural field conditions. However, controlled environment experiments have been extremely useful for quantifying responses, especially to temperature and photoperiod, and will continue to be so for large-scale phenotyping of valuable or limited stock of genetic material. For high and low temperature tolerance phenotyping protocols described in the papers quoted in this article are robust and applicable across a wide range of species and can use growth cabinets or temperature gradient tunnels. However, for traits related to drought and CO₂, where responses are the integrated effect of many processes through time, semi-controlled experiments are required for phenotyping. For water-use they include those such as the mini-lysimeters described by Vadez et al. (2008) while for CO₂ and temperature they include FACE and T-FACE systems (Kimball et al., 2008). Field experiments will also continue to be important if well designed around environmental gradients and with rigorous analysis based on previously quantified responses from controlled environments. For phenology (and model calibration), the analysis of existing multi-location trials data can also contribute valuable genotypic information.

As the capacity to downscale climate forecasts increases, and the mismatch between modeling scales decreases, there is an increasing need for models that purport to study impacts and adaptation options to use appropriate local cultivars in models rather than a

generic and usually improved cultivar. This is particularly true for crops such as sorghum, millet, upland rice and tropical legumes where diverse, usually photoperiod-sensitive cultivars are grown.

Two areas we need more crop science experiments on are the impact of high night temperatures and on water by temperature interactions, especially during flowering. Global increases in average temperature are associated with increases in minimum temperature and a number of studies have highlighted the negative effect of high minimum or night temperature on grain yield in rice (Peng et al., 2004; Nagarajan et al., 2010; Welch et al., 2010) and wheat (Prasad et al., 2008b). Despite the importance of high nighttime temperature in future climate, and its impact on growth and yield formation, the responses of respiration to temperature have not been thoroughly investigated. It is important to accurately define these thresholds and provide input to crop simulation models. Similarly, heat and drought stress often occur together, with water deficit through stomata closure exacerbating heat stress. Although both water deficit and temperature extremes affect seed-set, mechanisms are not necessarily the same and there are reports of interactive rather than additive effects (Shah and Paulsen, 2003; Prasad et al., 2011; Rang et al., 2011).

Another key area that we have not covered here, and one that is essential for climate change impacts and adaptation strategies, is crop science experiments for crop management options. Adaptation strategies need to be focused as much on crop management practices, particularly practices around water harvesting, water conservation and soil improvement, as on genetic enhancement of temperature and drought tolerance (Cooper et al., 2009; Hammer et al., 2006). For example, Cooper et al. (2009) have examined effects of small applications of fertilizer (micro-dosing), mulching, time of weeding and sowing date on yields in relation to expected changes in climate in East Africa. *Ex ante* modeling studies of adaptation options such as these will be increasingly important.

In conclusion, crop science experiments in both controlled and field environments are extremely useful for quantifying responses to photoperiod and temperature (development); quantifying responses to abiotic stresses such as temperature extremes and water deficit; identifying stages of development sensitive to environment and abiotic stress; and determining genotypic variability for these responses. The data generated from crop science experiments like those described above can be used for developing and improving crop simulation models to determine the impact of climate, management and genetics, and crop adaptation and mitigation strategies to changing climates. More research and investment is needed to develop fast and accurate phenotyping along with genetic data to help crop improvement for present and future climates.

References

- Agrawal, P.K., Kalra, N., Chander, S., Patha, H., 2006. Info crop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. I. Model description. *Agric. Syst.* 89, 1–25.
- Ahmed, F.E., Mutters, R.G., Hall, A.E., 1993. Interactive effects of high temperature and light quality on floral bud development in cowpea. *Aust. J. Plant Physiol.* 20, 661–667.
- Alagarswamy, G., Reddy, D.M., Swaminathan, G., 1998. Durations of the photoperiod-sensitive and -insensitive phases of time to panicle initiation in sorghum. *Field Crop Res.* 55, 1–10.
- Alagarswamy, G., Ritchie, J.T., 1991. Phasic development in CERES-sorghum model. In: Hodges, T. (Ed.), *Predicting Crop Phenology*. CRC Press, Boca Raton, pp. 143–152.
- Amato, M., Ritchie, J.T., 2002. Spatial distribution of roots and water uptake of maize (*Zea mays* L.) as affected by soil structure. *Crop Sci.* 42, 773–780.
- Baker, J.T., Allen, L.H., Boote, K.J., Jones, J.W., 1989. Responses of soybean to air temperature and carbon dioxide concentration. *Crop Sci.* 29, 98–105.
- Baker, J.T., Allen, L.H., Boote, K.J., Pickering, N.B., 1996. Assessment of rice responses to global climate change: CO₂ and temperature. In: Koch, G.N., Mooney, H.A. (Eds.), *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego, pp. 265–282.
- Bhatnagar-Mathur, P., Devi, M.J., Reddy, D.S., Lavanya, M., Vadez, V., Serraj, R., Yamaguchi-Shinozaki, K., Sharma, K.K., 2007. Stress-inducible expression of At DREB1A in transgenic peanut (*Arachis hypogaea* L.) increases transpiration efficiency under water-limiting conditions. *Plant Cell Rep.* 26, 2071–2082.
- Bierhuisen, J.F., Slatyer, R.O., 1965. Effect of atmospheric concentration of water vapor and CO₂ in determining transpiration photosynthesis relationships of cotton leaves. *Agric. Meteorol.* 2, 259–270.
- Bonhomme, R., Derieux, M., Edmeades, G.O., 1994. Flowering of diverse maize cultivars in relation to temperature and photoperiod in multilocation field trials. *Crop Sci.* 34, 156–164.
- Carberry, P.S., Ranganathan, R., Reddy, L., Chauhan, Y.S., Robertson, M.J., 2001. Predicting growth and development of pigeonpea: flowering response to photoperiod. *Field Crop Res.* 69, 151–162.
- Challinor, A., Wheeler, T.R., 2008a. Crop yield reduction in the tropics under climate change: processes and uncertainties. *Agric. For. Meteorol.* 148, 343–356.
- Challinor, A.J., Wheeler, T.R., 2008b. Using a crop model ensemble to quantify CO₂ stimulation of water-stressed and well watered groundnut. *Agric. For. Meteorol.* 148, 1062–1077.
- Challinor, A.J., Wheeler, T.R., Craufurd, P.Q., Ferro, C.A.T., Stephenson, D.B., 2007. Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. *Agric. Ecosyst. Environ.* 119, 190–204.
- Challinor, A.J., Wheeler, T.R., Craufurd, P.Q., Slingo, J.L., Grimes, D.I.F., 2004. Design and optimisation of a large-area process-based model for annual crops. *Agric. For. Meteorol.* 124, 99–120.
- Challinor, A.J., Wheeler, T.R., Craufurd, P.Q., Slingo, J.M., 2005. Simulation of the impact of high temperature stress on annual crop yields. *Agric. For. Meteorol.* 135, 180–189.
- Challinor, A.J., Wheeler, T.R., Hemming, D., Upadhyaya, H.D., 2009. Ensemble yield simulations: crop and climate uncertainties, sensitivity to temperature and genotypic adaptation to climate change. *Clim. Res.* 38, 117–127.
- Claassen, M.M., Shaw, R.H., 1970. Water-deficit effects on corn. II. Grain composition. *Agron. J.* 62, 652–655.
- Clerget, B., Dingkuhn, M., Chantreau, J., Hemberger, J., Louarn, G., Vaksmann, M., 2004. Does panicle initiation in tropical sorghum depend on day-to-day change in photoperiod? *Field Crop Res.* 88, 21–37.
- Cohen, Y., Alchanatis, V., Meron, M., Saranga, Y., Tsipris, J., 2005. Estimation of leaf water potential by thermal imagery and spatial analysis. *J. Exp. Bot.* 56, 1843–1852.
- Collinson, S.T., Ellis, R.H., Summerfield, R.J., Roberts, E.H., 1992. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of rice (*Oryza sativa* L.). *Ann. Bot.* 70, 339–346.
- Collinson, S.T., Summerfield, R.J., Ellis, R.H., Roberts, E.H., 1993. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of soybeans (*Glycine max* (L.) Merrill). *Ann. Bot.* 71, 389–394.
- Cooper, M., Podlich, D.W., Smith, O.S., 2005. Gene-to-phenotype models and complex trait genetics. *Aust. J. Agric. Res.* 56, 895–918.
- Cooper, P., Rao, K.P.C., Singh, P., Dimes, J., Traore, P.S., Rao, K., Dixit, P., Twomlow, S.J., 2009. Farming with current and future climate risk: advancing a hypothesis of hope for rainfed agriculture in the semi-arid tropics. *J. SAT Agric Res.* 7, 19.
- Craufurd, P.Q., Bojang, M., Wheeler, T.R., Summerfield, R.J., 1998. Heat tolerance in cowpea: effect of timing and duration of heat stress. *Ann. Appl. Biol.* 133, 257–267.
- Craufurd, P.Q., Mahalakshmi, V., Bidinger, F.R., Muku, S.Z., Chantreau, J., Omanga, P.A., Qi, A., Roberts, E.H., Ellis, R.H., Summerfield, R.J., 1999. Adaptation of sorghum: characterisation of genotypic flowering responses to temperature and photoperiod. *Theor. Appl. Gen.* 99, 900–911.
- Craufurd, P.Q., Prasad, P.V.V., Kakani, V.G., Wheeler, T.R., Nigam, S.N., 2003. Heat tolerance in groundnut. *Field Crop Res.* 80, 63–77.
- Craufurd, P.Q., Qi, A., 2001. Photothermal adaptation of sorghum (*Sorghum bicolor*) in Nigeria. *Agric. For. Meteorol.* 108, 199–211.
- Craufurd, P.Q., Wheeler, T.R., 2009. Climate change and the flowering time of annual crops. Flowering newsletter review. *J. Exp. Bot.* 60, 2529–2539.
- Dardanelli, J.L., Bachmeier, O.A., Sereno, R., Gil, R., 1997. Rooting depth and soil water extraction patterns of different crops in a silty loam haplustoll. *Field Crops Res.* 54, 29–38.
- Dardanelli, J.L., Ritchie, J.T., Calmon, M., Andriani, J.M., Collino, D.J., 2004. An empirical model for root water uptake. *Field Crops Res.* 87, 59–71.
- Devi, J.M., Sinclair, T.R., Vadez, V., Krishnamurthy, L., 2009. Peanut genotypic variation in transpiration efficiency and decrease transpiration during progressive soil drying. *Field Crops Res.* 114, 280–285.
- Devi, M.J., Sinclair, T.R., Vadez, V., 2010. Genotypic variation in peanut for transpiration response to vapor pressure deficit. *Crop Sci.* 50, 191–196.
- Dingkuhn, M., 1995. Climatic determinants of irrigated rice performance in the Sahel. III. Characterizing environments by simulating crop phenology. *Agric. Syst.* 48, 435–456.
- Dingkuhn, M., Asch, F., 1999. Phenological responses of *Oryza sativa*, *O. glaberrima* and inter-specific rice cultivars on a toposequence in West Africa. *Euphytica* 110, 109–126.
- Ellis, R.H., Collinson, S.T., Hudson, D., Patefield, W.M., 1992. The analysis of reciprocal transfer experiments to estimate duration of the photoperiod-sensitive and photoperiod insensitive phases of plant development: an example in soybean. *Ann. Bot.* 70, 87–92.

- Erskine, W., Ellis, R.H., Summerfield, R.J., Roberts, E.H., Hussain, A., 1990. Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection. *Theor. Appl. Genet.* 80, 193–199.
- Flower, D.J., 1996. Physiological and morphological features determining the performance of the sorghum landraces of northern Nigeria. *Exp. Agric.* 32, 129–141.
- Folliard, A., Traoré, P.C.S., Vaxsmann, M., Kouressy, M., 2004. Modeling of sorghum response to photoperiod: a threshold-hyperbolic approach. *Field Crops Res.* 89, 59–70.
- Gholipour, M., Prasad, P.V.V., Mutava, R.N., Sinclair, T.R., 2010. Genetic variability of transpiration response to vapor pressure deficit among sorghum genotypes. *Field Crops Res.* 119, 85–90.
- Hatfield, J.T., Boote, K.J., Fay, P., Hahn, L., Izaurralde, C., Kimball, B.A., Mader, T., Morgan, J., Ort, D., Polley, W., Thomson, A., Wolfe, D., 2008. Chapter 2. Agriculture. In: *The Effect of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research.* Washington, DC, USA, 360 pp.
- Hall, A.E., 1993. Physiology and breeding for heat tolerance in cowpea and comparisons with other crops. In: Kuo, G.C. (Ed.), *Adaptation of Food Crops to Temperature and Water Stress.* AVRDC, Taipei, Taiwan, pp. 271–284.
- Hamblin, A.P., Tennant, D., 1987. Root length density and water uptake in cereals and grain legumes: how well are they correlated. *Aust. J. Agric. Res.* 38, 513–527.
- Hammer, G.L., Cooper, M.C., Tardieu, F.T., Welch, S.W., Walsh, B.M., van Eeuwijk, F., Chapman, S.C., Podlich, D.P., 2006. Models for navigating biological complexity in breeding improved crop plants. *Trends Plant Sci.* 11, 587–593.
- Jagadish, S.V.K., Craufurd, P.Q., Wheeler, T.R., 2007. High temperature stress and spikelet fertility in rice (*Oryza sativa* L.). *J. Exp. Bot.* 58, 1627–1635.
- Jagadish, S.V.K., Cairns, J., Lafitte, R., Wheeler, T.R., Price, A.H., Craufurd, P.Q., 2010. Genetic analysis of heat tolerance at anthesis in rice (*Oryza sativa* L.). *Crop Sci.* 50, 1633–1641.
- Jagadish, S.V.K., Craufurd, P.Q., Wheeler, T.R., 2008. Phenotyping parents of mapping populations of rice (*Oryza sativa* L.) for heat tolerance during anthesis. *Crop Sci.* 48, 1140–1146.
- Jiang, C., Edmeades, G.O., Armstead, I., Lafitte, H.R., Hayward, M.D., Hoisington, D., 1999. Genetic analysis of adaptation differences between highland and lowland tropical maize using molecular markers. *TAG Theor. Appl. Genet.* 99, 1106–1119.
- Jones, J.W., Hoogenboom, G., Porter, C.H., Boote, K.J., Batchelor, W.D., Hunt, L.A., Wilkens, P.W., Singh, U., Gijsman, A.J., Ritchie, J.T., 2003. The DSSAT cropping system model. *Eur. J. Agron.* 18, 1708–1716.
- Jung, C., Muller, A.E., 2009. Flowering time control and applications in plant breeding. *Trends Plant Sci.* 14, 563–573.
- Katayama, K., Ito, O., Adu-gyamfi, J.J., Rao, T.P., 2000. Analysis of Relationship between Root Length Density and Water Uptake by roots of Five Crops Using Minirhizotron in the Semi-Arid Tropics. Reprinted from JARQ, vol. 34, no. 2.
- Keating, B.A., Kiberry, P.S., Hammer, G.L., Probert, M.E., Robertson, M.J., Holzworth, D., Huth, N.I., Hargreaves, J.N.G., Meinke, H., Hochman, Z., Mclean, G., Verburg, K., Snow, V., Dimes, J.P., Silburn, M., Wang, E., Brown, S., Bristow, K.L., Asseng, S., Chapman, S., Mccown, R.L., Freebairn, D.M., Smith, C.J., 2003. An overview of APSIM, a model designed for farming systems simulation. *Eur. J. Agron.* 18, 267–288.
- Kholova, J., Hash, C.T., Kakkera, A., Kocova, M., Vadez, V., 2010a. Constitutive water-conserving mechanisms are correlated with the terminal drought tolerance of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *J. Exp. Bot.* 61, 369–377.
- Kholova, J., Hash, C.T., Kumar, P.L., Yadav, R.S., Kocova, M., Vadez, V., 2010b. Terminal drought-tolerant pearl millet [*Pennisetum glaucum* (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. *J. Exp. Bot.* 61, 1431–1440.
- Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J., Smith, D., 2008. Infrared heater arrays for warming ecosystem field plots. *Global Change Biol.* 14, 309–320.
- Lafolie, F., Bruckier, L., Tardieu, F., 1991. Modeling root water potential and soil-root water transport. 1. Model presentation. *Soil Sci. Soc. Am. J.* 55, 1203–1212.
- Lobell, D., Field, C., 2007. Global scale climate-crop yield relationships and the impacts of recent warming. *Environ. Res. Lett.* 2.
- Long, S., Ort, D., 2010. More than taking the heat: crops and global change. *Curr. Opin. Plant Biol.* 13, 241–248.
- Matsui, T., Namuco, O.S., Ziska, L.H., Horie, T., 1997. Effect of high temperature and CO₂ concentration on spikelet sterility in indica rice. *Field Crops Res.* 51, 213–219.
- Matsui, T., Omasa, K., Horie, T., 2001. The difference in sterility due to high temperatures during the flowering period among *japonica* rice varieties. *Plant Prod. Sci.* 4, 90–93.
- Matthews, R., Kropff, M., Bachelet, D., Van Laar, H., 1995. Modeling the Impact of Climate Change on Rice Production in Asia. CAB, Wallingford.
- Messina, C.D., Hammer, G.L., Dong, G., Podlich, D., Cooper, M., 2009. Modelling crop improvement in a G × E × M framework via gene-trait-phenotype relationships. In: Sadras, V., Calderini, D. (Eds.), *Crop Physiology: Interfacing with Genetic Improvement and Agronomy.* The Netherlands, Elsevier, pp. 235–265.
- Mohammed, A.R., Tarpley, L., 2009. High nighttime temperatures affect rice productivity through altered pollen germination and spikelet fertility. *Agric. For. Meteorol.* 149, 999–1008.
- Monteith, J.L., 1986. How do crops manipulate supply and demand? *Philos. Trans. R. Soc. Lond. A* 316, 245–259.
- Mutters, R.G., Hall, A.E., 1992. Reproductive responses of cowpea to high temperature during different night periods. *Crop Sci.* 32, 202–206.
- Nagarajan, S., Jagadish, S.V.K., Prasad, A.S.H., Thomar, A.K., Anand, A., Pal, M., Agrawal, P.K., 2010. Local climate affects growth, yield and grain quality of aromatic and non-aromatic rice in northwestern India. *Agric. Ecosyst. Environ.* 138, 274–281.
- Nakagawa, H., Horie, T., Matsui, T., 2003. Effects of climate change on rice production and adaptive technologies. In: Mew, T., et al. (Eds.), *Rice Science: Innovations and Impact for Livelihood.* IRRI/Chinese Academy of Engineering/Chinese Academy of Agricultural Sciences, Manila, pp. 635–657.
- Nelson, G.C., Rosegrant, M.W., Palazzo, A., Gray, I., Ingersoll, C., Robertson, R., Tokgoz, S., Zhu, T., Sulser, T.B., Ringler, C., Msangi, S., You, L., 2010. *Food Security, Farming and Climate Change to 2050.* IFPRI, Washington.
- Nielsen, C.L., Hall, A.E., 1985. Responses of cowpea (*Vigna unguiculata* (L.) Walp.) in the field to high night air temperatures during flowering. 1. Thermal regimes of production regions and field experimental system. *Field Crops Res.* 10, 167–179.
- O'Toole, J.C., 1982. Adaptation to drought-prone environments. In: *Drought Resistance in Cereals with Emphasis on Rice.* IRRI, Manila, pp. 95–213.
- Ogunlela, V.B., Eastin, J.D., 1984. Effect of elevated night temperature during panicle development on sorghum (*Sorghum bicolor* L.) yield components. *Cereal Res. Commun.* 12, 3–4.
- Passioura, J.B., 1983. Roots and drought resistance. *Agric. Water Manag.* 7, 265–280.
- Peng, S., Huang, J., Sheehy, J.E., Laza, R.C., Visperas, R.M., Zhong, X., Centeno, G.S., Khush, G.S., Cassman, K.G., 2004. Rice yields decline with higher night temperature from global warming. *Proc. Natl. Acad. Sci. U.S.A.* 101, 9971–9975.
- Prasad, P.V.V., Craufurd, P.Q., Summerfield, R.J., 1999. Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Ann. Bot.* 84, 381–386.
- Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., 2006a. Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. *Agric. For. Meteorol.* 139, 237–251.
- Prasad, P.V.V., Boote, K.J., Allen, L.H., Sheehy, J.E., Thomas, J.M.G., 2006b. Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. *Field Crops Res.* 95, 398–411.
- Prasad, P.V.V., Boote, K.J., Allen, L.H., Thomas, J.M.G., 2002. Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). *Global Change Biol.* 8, 710–721.
- Prasad, P.V.V., Boote, K.J., Allen, L.H., Thomas, J.M.G., 2003. Super-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L.) reproductive processes and yield at both ambient and elevated carbon dioxide. *Global Change Biol.* 9, 1775–1787.
- Prasad, P.V.V., Craufurd, P.Q., Kakani, V.G., Wheeler, T.R., Boote, K.J., 2001. Influence of temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in groundnut (*Arachis hypogaea* L.). *Aust. J. Plant Physiol.* 28, 233–240.
- Prasad, P.V.V., Craufurd, P.Q., Summerfield, R.J., Wheeler, T.R., 2000. Effects of short episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). *J. Exp. Bot.* 51, 777–784.
- Prasad, P.V.V., Pispipati, S.R., Ristic, Z., Bukovnik, U., Fritz, A.K., 2008a. Impact of nighttime temperature on physiology and growth of spring wheat. *Crop Sci.* 48, 2372–2380.
- Prasad, P.V.V., Pispipati, S.R., Momcilovic, I., Ristic, Z., 2011. Independent and combined effect of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. *J. Agron. Crop Sci.* doi:10.1111/j.1439-037X.2011.00477.x.
- Prasad, P.V.V., Pispipati, S.R., Mutava, R.N., Tuinstra, M.R., 2008b. Sensitivity of grain sorghum to high temperature stress during reproductive development. *Crop Sci.* 48.
- Rang, Z.W., Jagadish, S.V.K., Zhou, Q.M., Craufurd, P.Q., Heuer, S., 2011. Effect of heat and drought stress on pollen germination and spikelet fertility in rice. *Environ. Exp. Bot.* 70, 58–65.
- Ratnakumar, P., Vadez, V., Nigam, S.N., Krishnamurthy, L., 2009. Assessment of transpiration efficiency in peanut (*Arachis hypogaea* L.) under drought by lysimetric system. *Plant Biol.* 11, 124–130.
- Ray, J.D., Sinclair, T.R., 1998. The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. *J. Exp. Bot.* 49, 1381–1386.
- Roberts, E.H., Qi, A., Ellis, R., Summerfield, R.J., Lawn, R.J., Shanmugasundaram, S., 1996. Use of field observations to characterise genotypic flowering responses to photoperiod and temperature: a soybean exemplar. *Theor. Appl. Genet.* 93, 519–533.
- Salem, M.A., Kakani, V.G., Koti, S., Reddy, K.R., 2007. Pollen-based screening of soybean genotypes for high temperatures. *Crop Sci.* 47, 219–231.
- Shah, N.H., Paulsen, G.M., 2003. Interaction of drought and high temperature on photosynthesis and grain-filling of wheat. *Plant Soil* 257, 219–226.
- Sinclair, T.R., Hammer, G.L., van Oosterom, E.J., 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. *Funct. Plant Biol.* 32, 945–952.
- Sinclair, T.R., Hinson, K., 1992. Soybean flowering response to the long-juvenile trait. *Crop Sci.* 32, 1242–1248.
- Sinclair, T.R., Ludlow, M.M., 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. *Aust. J. Plant Physiol.* 13, 329–341.
- Sinclair, T.R., Messina, C.D., Beatty, A., Samples, M., 2010. Assessment across the United States of the benefits of altered soybean drought traits. *Agron. J.* 102, 475–482.
- Sinclair, T.R., Muchow, R.C., 2001. System analysis of plant traits to increase grain yield on limited water supplies. *Agron. J.* 93, 263–270.
- Sinclair, T.R., Seligman, N., 2000. Criteria for publishing papers on crop modeling. *Field Crops Res.* 68, 165–172.

- Sinclair, T.R., Zwieniecki, M.A., Holbrook, N.M., 2008. Low leaf hydraulic conductance associated with drought tolerance in soybean. *Physiol. Plant.* 132, 446–451.
- Soltani, A., Khoie, F.R., Ghassemi-Golezani, K., Moghaddam, M., 2000. Thresholds for chickpea leaf expansion and transpiration response to soil water deficit. *Field Crops Res.* 68, 205–210.
- Steduto, P., Hsiao, T.C., Raes, D., Fereres, E., 2009. AquaCrop-The FAO crop model to simulate response to water. I. Concepts and underlying principles. *Agron. J.* 101, 426–437.
- Tao, F., Zhang, Z., 2010. Adaptation of maize production to climate change in North China Plain: quantify the relative contributions of adaptation options. *Eur. J. Agron.* 33, 103–116.
- Vadez, V., Rao, S., Kholova, J., Krishnamurthy, L., Kashiwagi, J., Ratnakumar, P., Sharma, K.K., Bhatnagar-Mathur, P., Basu, P.S., 2008. Roots research for legume tolerance to drought: *Quo vadis?* *J. Food Legumes* 21, 77–85.
- Vadez, V., Rao, S., Sharma, K.K., Bhatnagar Mathur, Devi, J.M., 2007. DREB1A allows for more water uptake in groundnut by a large modification in the root/shoot ratio under water deficit. *Int. Arachis Newslett.* 27, 27–31.
- Vadez, V., Sinclair, T.R., 2001. Leaf ureide degradation and the N₂ fixation tolerance to water deficit in soybean. *J. Exp. Bot.* 52, 153–159.
- Vaksmann, M., Traore, S.B., Kouressy, M., Coulibaly, H., Reyniers, F.-N., 1998. Etude du developpement d'un sorgho photoperiodique du Mali. In: Bacci, L., Reyniers, F.-N. (Eds.), *Le futur des cereales photoperiodiques pour une production durable en afrique tropicale semi-aride*. Ce.S.I.A and CIRAD, Florence, pp. 109–122.
- Vergara, B.S., Chang, T.T., 1976. The Flowering Response of the Rice Plant to Photoperiod: A Review of the Literature, 8 ed. 3rd Int. Rice Res. Inst. Tech. Bull., IRRI, Los Banos.
- Welch, J.R., Vincent, J.R., Auffhammer, M., Moyae, P.F., Dobermann, A., Dawe, D., 2010. Rice yields in tropical/subtropical Asia exhibit large but opposing sensitivities to minimum and maximum temperatures. *Proc. Natl. Acad. Sci. U.S.A.*, doi:10.1073/pnas.1001222107.
- Welch, S., Dong, Z., Roe, J., 2004. Modelling gene networks controlling transition to flowering in Arabidopsis. In: 4th International Crop Science Congress, Brisbane, Australia, p. 20.
- Wheeler, T.R., Craufurd, P.Q., Ellis, R.H., Porter, J.R., Prasad, P.V.V., 2000. Temperature variability and the yield of annual crops. *Agric. Ecosyst. Environ.* 82, 159–167.
- Wheeler, T.R., Hong, T.D., Ellis, R.H., Batts, G.R., Morison, J.L., Hadley, P., 1996. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO₂. *J. Exp. Bot.* 47, 623–630.
- White, J.W., Hoogenboom, G., 2003. Gene-based approaches to crop simulation: past experiences and future opportunities. *Agron. J.* 95, 52–64.
- Yoshida, S., Satake, T., Mackill, D., 1981. High temperature stress in rice. *IRRI Res. Pap. Ser.* 67, 1–15.
- Zaman-Allah, M., Jenkinson, D.M., Vadez, V., 2011a. Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. *Funct. Plant Biol.* 38, 270–281.
- Zaman-Allah, M., Jenkinson, D.M., Vadez, V., 2011b. A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpea. *J. Exp. Bot.* 62, 4239–4252.